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Ecological Niches and Diversity Maintenance

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1. Introduction

Why do some places have much higher diversity than others? Explaining patterns of species diversity on the earth is a problem of long-standing for ecologists. Numerous diversity patterns have been documented [1], but the mechanisms behind these patterns remain poorly understood. If we knew the mechanisms, surer decisions in conservation and management would be possible. Understanding can be sought in many different ways. A dominant approach in community ecology is to search for explanations through the study of species interactions [2, 3]. This approach is motivated by the competitive exclusion principle, which suggests that there are limits to how similar species can be in their ecology while coexisting with one another in a stable way [2-6]. However, the competitive exclusion principle is challenged by the existence of many highly diverse communities of seemingly similar species. A response to this challenge is neutral theory, which postulates that many coexisting species are ecologically identical in respects that matter, and do not coexist stably. Instead, they undergo random walks to extinction, with diversity replenished by speciation, and immigration of species from other areas [7]. The neutral theory has been successful in predicting some diversity patterns in nature [8], but fails in other areas [9-12], and is limited in the nature of the predictions that it can produce [13].

Other responses to the diversity challenge take the competitive exclusion principle seriously, although with a broad definition of stability [5]. These responses seek to understand the various ways that species differ from one another, how these differences structure species interactions and ultimately contribute to diversity maintenance in terms of species coexistence mechanisms [3, 5, 14, 15]. Traditional approaches focus on the differences between similar species in the ways they exploit resources, with some attention to the role of natural enemies in mediating or modifying interactions. New developments emphasize that the relationships that species have with their natural enemies are potentially just as important for diversity maintenance as their relationships with resources, and can have very similar outcomes [16]. Other directions focus on structuring and variation in the physical environment, emphasizing that the abilities of similar species to coexist with one another may have much to do with physical environmental structure [15, 17-19].

Testing diversity maintenance hypotheses in nature is a vexing challenge [3]. Data are often limited and manipulating systems experimentally for testing diversity maintenance questions poses serious difficulties. Moreover, devising definitive tests of mechanisms has been problematic [20, 21]. However, work on coexistence mechanisms in variable

environments has led to methods of quantifying the strength of coexistence mechanisms, and these quantifications have suggested definitive tests of mechanisms in nature [22]. Implementing these new methods comes with all the usual difficulties of ecological field manipulation, but the ability to focus on surer methods [20] may ultimately lead to the kind of focus in experimental technique that leads to breakthroughs.

In spite of the difficulty of understanding which coexistence mechanisms are active in a given system, enough commonalities exist between different mechanisms of stable coexistence to allow some general advice for conservation and management. Although we are a long way from truly understanding diversity maintenance, we have enough knowledge to suggest a number of areas where caution is needed. Species should not be managed in isolation. Factors improving the situation for one set of species may degrade it for others. Maintaining trophic structure, physical environmental structure, disturbance regimes, and spatial connectivity are all common sense ideas that receive support from existing understanding of diversity maintenance mechanisms.

2. Fitness differences, niches and coexistence

When we consider how species interactions limit diversity, an important concept is the average fitness of a species as a whole, for this average fitness determines a species' ability to dominate other species with which it interacts. This concept is not to be confused with the fitness of a genotype or individual organism. The most common use of the idea of fitness is for genotypes or individual alleles of a gene, where its use is often relative, to predict the survival of a genotype or allele compared with others [23, 24]. Ecologists, however, often give fitness an absolute meaning as the performance of an individual organism, and this individual-level fitness is often measured as the total number of offspring that an individual leaves in its life time [25]. An alternative and more pragmatic meaning is its contribution to the population over a defined period of time through its own survival and reproduction [23]. Fitness at the species level applies in a similar relative context to fitness of a genotype or allele, but in this usage fitness specifies the relative degree of adaptedness of a species compared to others having a similar way of life and living in the same area, i.e. this fitness measure is to relative other species in the same guild, living in the same area [20].

When this species-level fitness measure is applied to problems of species coexistence, it assumes that the area of land in question is large enough for populations to be closed on an ecological timescale [5]. Then the fitness measure, which we denote κ , determines the degree of adaptedness of a species to the conditions applicable on that area of land. If the species in a guild cannot coexist with one another, then it is the species with the largest value of κ that persists, excluding others. More generally, the κ values rank the species in terms of their adaptation to the environment, and in essence rank the species in terms of how secure their persistence is when interacting with the others species in the guild.

2.1 The MacArthur consumer-resource model

A program to measure average fitness measures in nature has been proposed [26], but at the present time, these measures are easier to define in models. We consider the model of MacArthur [27] where a guild of animal species consume common biological resources in a lower trophic level, as reworked by Chesson [5, 28]. This model has had a key role in the development of ideas on resource partitioning for animal guilds (Table 1). Fig. 1 diagrams the foodweb being modeled, and Table 1 specifies the equations.

<p>MacArthur Consumer-resource Equations</p>	$\frac{1}{N_j} \frac{dN_j}{dt} = \sum_l c_{jl} R_l v_l - \mu_j$ <p>(consumer equation)</p> $\frac{1}{R_l} \frac{dR_l}{dt} = r_l^R (1 - \alpha_l^R R_l) - \sum_j N_j c_{jl}$ <p>(resource equation)</p>
<p>Average fitness measure</p>	$\kappa_j = \frac{1}{s_j} \left(\underbrace{\sum_l c_{jl} K_l^R v_l}_{\text{Harvesting ability}} - \underbrace{\mu_j}_{\text{Maintenance requirement}} \right)$ $s_j = \sqrt{\underbrace{\left(\sum_l c_{jl}^2 v_l K_l^R / r_l^R \right)}_{\text{Sensitivity}}}$
<p>Overlap measure</p>	$\rho = \sum_l \frac{c_{jl} v_l K_l^R c_{kl}}{r_l^R} / s_j s_k$
<p>Derived Lotka-Volterra Equations</p>	$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2)$ $\frac{1}{N_2} \frac{dN_2}{dt} = r_2 (1 - \alpha_{21} N_1 - \alpha_{22} N_2)$
<p>Notation</p>	<p>N_j: Density of (consumer) species j. R_l: Density of resource l. c_{jl}: Consumption rate of resource l by species j. v_l: unit value of resource l. μ_j: resource maintenance requirement of species j. r_l^R: Maximum growth rate of resource l. α_l^R: Intraspecific competition for resource l $1 / K_l^R$, the carrying capacity of the resource. α_{ij}: Coefficient for competition for the effect of species j on species i</p>

Table 1. MacArthur’s consumer-resource equations

The fitness measure κ derived from this model involves three things (Table 1). The first is the ability of a species to harvest resources. This is the total resource intake of a species when its resources are at their carrying capacities.

This quantity, therefore, is a maximum resource harvesting rate. Subtracted from it is the resource maintenance requirement, which is the level of resource intake needed for a per capita growth rate of exactly zero, i.e. it is the resource intake that gives an individual organism a fitness of 1, which means that that one individual is replaced by exactly one individual on average in one unit of time. The maximum resource intake, less the maintenance requirement, measures the ability of a species to meet its needs, and is called the net maximum harvesting rate. Finally, the net maximum harvesting rate is divided by a quantity s which measures the sensitivity of the growth rate of the species to changes in resource availability, as discussed in detail by Chesson [20]. The resulting quantity is the average fitness measure κ (Table 1).

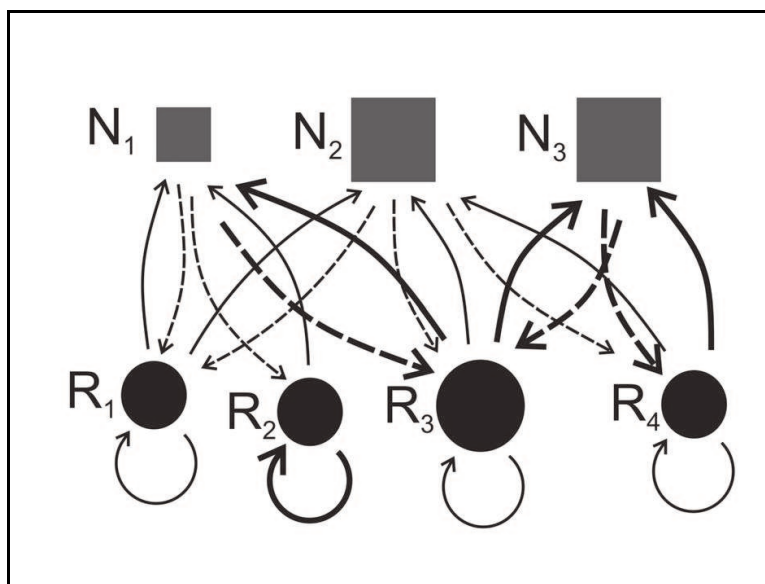


Fig. 1. Foodweb in the MacArthur model. Squares are the focal guild members and circles are resources. Arrows indicate the directions of effects of one species on another, with thickness differences indicating differences in strengths of these effects. The feedback loops for guild members come from links from a square to a circle back to a square. Circular loops for resources indicate resource self-limitation.

Although this fitness measure κ may seem intuitively reasonable, the real test is its ability to predict the outcome of the interactions of this species with others in the same guild. The measure κ has this desired property because it is related to competition coefficients derived from the MacArthur consumer-resource model. These competition coefficients are denoted α_{ij} giving the effect of interspecific competition from species j onto species i , and α_{jj} for intraspecific competition within species j . They measure the feedback loops illustrated in Fig. 1 from one species to another, and from one species back to itself. Moreover, when resource dynamics are fast relative to consumer dynamics, e.g. because resource species have much shorter generation times, the MacArthur consumer-resource model reduces to the Lotka-Volterra competition model defined by these competition coefficients [5] – see Table 1 for the two-species case. Of most importance, the ratio of interspecific competition to intraspecific competition is related to the ratio of the κ values:

$$\frac{\kappa_j}{\kappa_i} \rho = \frac{\alpha_{ij}}{\alpha_{ji}}, \quad (1)$$

where the quantity ρ measures overlap in resource use between species i and species j [5]. Fundamentally, we see that the ratio of the fitness measures determines how much one species affects another, compared with how much it affects itself. Understandably, however, relative fitness alone does not do this. It is most important to know how much the species interact with one another also. Thus, the fitness ratio is multiplied by the overlap measure, ρ , which is on a scale from 0 to 1, with 1 meaning complete overlap and 0 meaning no overlap.

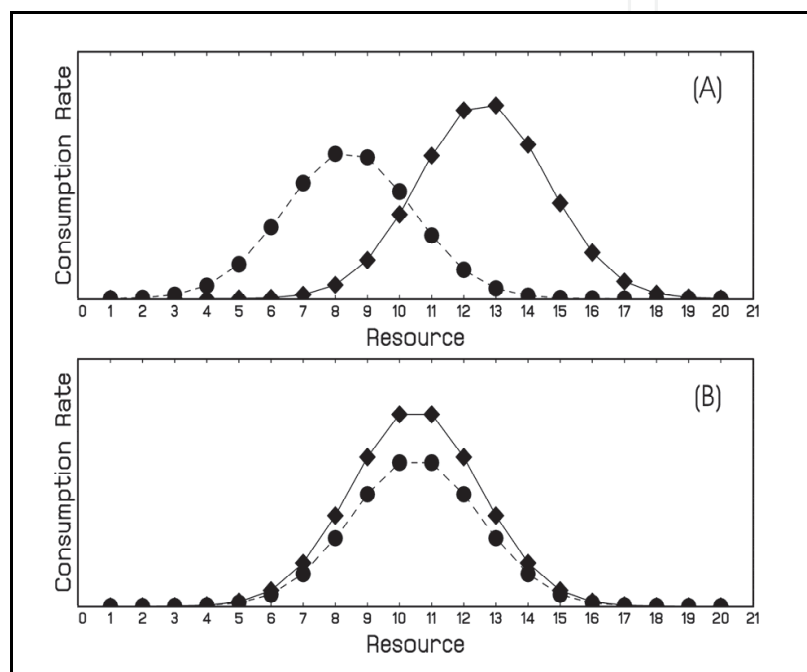


Fig. 2. Niche relationships of two species, in terms of the consumption rates on limiting resources. (A) Partial overlap in resource use, $\rho = 0.33$. (B) Complete overlap, $\rho = 1$.

Fig. 2 shows the niche relationships of two species as specified by their consumption rate curves for both partial overlap and complete overlap, while Table 1 shows how this overlap measure is calculated. The difference in the heights of the consumption rate curves does not affect the overlap, but is a factor explaining the difference between the fitnesses, κ .

Interpreting this result is simplest in the case of two species competing with one another. If expression (1) is greater than 1, then species j excludes i from the system. In terms of competition coefficients, this means that species j places less limitation on its own growth as it increases in abundance than it places on the growth of the species i . Thus, species j continues increasing in abundance beyond the point that the growth of species i becomes negative.

In terms of the fitness ratio and overlap measure, if the species overlap completely in resource use, then species j excludes i if it simply has a higher fitness than species i . However, with less than complete overlap, this fitness ratio needs to be discounted by the degree of overlap to determine if species j can exclude i . For example, if $\rho = 2/3$, then the fitness ratio needs to be more than $3/2$, rather than just more than 1. Said another way, if one species is fitter than another, it only harms that other species to the extent that they

overlap in resource use. As we shall see below, this statement generalizes to all forms of overlap associated with interactions between the species.

In the case where neither of two competing species can exclude the other, they coexist. For two species labeled 1 and 2, this means that expression (1) must be less than 1 for $(i, j) = (1, 2)$ and $(2, 1)$, discounting the unlikely boundary case of equality with 1, discussed below. This condition can be rearranged to

$$\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}, \quad (2)$$

and shows that overlap, ρ , places constraints on how different the average fitness measures for the two species can be and still allow coexistence. Simply put, the more similar the species are in resource use (the closer ρ is to 1), the more similar they have to be in average fitness for coexistence to occur. In opposite terms, the more different the species are in resource use, the more different they must be in average fitness before one excludes the other.

This analysis of MacArthur's model yields some important general lessons. The competitive exclusion principle holds that species that are very similar in their ecology should have difficulty coexisting. Similarity in ecology within the MacArthur model can be interpreted as meaning a ρ value near 1, i.e. high overlap in resource use. Difficulty in coexisting can now be interpreted as meaning that the species have to be evenly matched in average fitness if they are to coexist, i.e. if one species gets a small edge in average fitness over the other, then exclusion will occur.

These findings for the MacArthur model generalize to others [5, 29], and they highlight two different sorts of similarity between species. The first is similarity in average fitness, i.e. having κ values near to each other. As discussed above, the κ values allow ranking of overall adaptation to the environment. Almost by definition, having similar κ values is favorable to species coexistence. However, similarity in κ values is a very different concept from similarity in way of life, or similarity in niches, when niches are defined in terms of the way of life of a species [5, 30]. In the MacArthur model, similarity in way of life reduces to similarity in resource use, which then determines how much the species interact with one another. Thus, similarity in niches constrains differences in average fitness compatible with coexistence, by conditions (2).

Looked at another way, we can think of these similarities and differences as relating to average performance compared with performance under specific conditions. Species 1 and 2 in Fig. 2(A) have very different performance under specific conditions; for example, species 1 derives very little benefit from resources 13 to 17, instead gaining most benefit from resources 5 to 12 while species 2 has an opposite pattern. The average performances of the species, which depend on the heights of the curves in the figure, are nowhere near as different as their performances for most specific resources.

Differences in performance under specific conditions lead to tolerance of average performance differences. For example, in the MacArthur model, specific-condition differences give a small value of ρ , and thus wide tolerance in the κ ratio. More generally, the nature of these specific differences is very important. They must relate directly or indirectly to separation of feedback loops because it is separation of these feedback loops that makes it possible for intraspecific competition to exceed interspecific competition, the key to coexistence. With the MacArthur model, the measure ρ is a specific measure of the degree of separation of those feedback loops. Multiplication by the fitness ratio adjusts the

degree of separation of those loops for the relative degrees of resource shortage that the two species can tolerate due to their overall adaptation to the environment, to give the competition coefficient ratio (1).

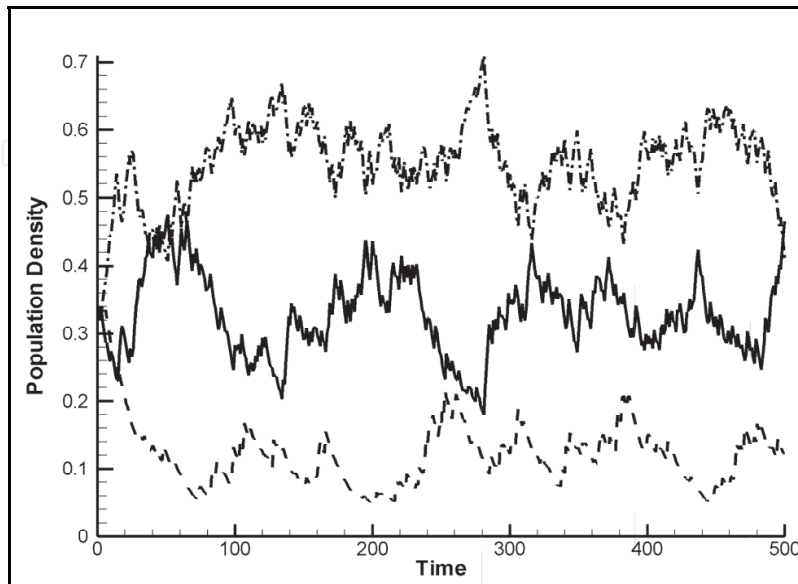


Fig. 3. Simulation showing species coexisting stably according to the lottery competition in a temporally varying environment. Note that each species shows a strong tendency to recover from fluctuations to low density.

2.2 Stable versus neutral coexistence

When the conditions (2) above are satisfied in the MacArthur model, the result is stable coexistence in the sense that if either species is perturbed to low density, it recovers from that low density state. In general, the MacArthur model leads to a stable equilibrium point. However, by stable coexistence, a stable equilibrium is not implied. Instead, the requirement is recovery of each species from low density, which is fully compatible with fluctuating coexistence, as illustrated in Fig. 3. Indeed, Fig. 3 illustrates stable coexistence in the lottery model [31], which requires temporal fluctuations for stable coexistence to occur. i.e. it is an example of fluctuation-dependent coexistence [32], as discussed below under variation in time and space. Neutral models, on the other hand, do not allow stable coexistence. Instead, they are characterized by having average fitnesses the same for all species. Thus, all species have the same κ values, and the niche overlap measures ρ between all pairs of species are all 1. In general, the key assumption of neutral models is stronger: it is that the species identity of an individual has no bearing on how it is affected by any other individual or how it affects other individuals [33]. However, this stronger assumption is no particular concern here. With equal average fitnesses and complete niche overlap, in the MacArthur model expression (1) is exactly equal to 1, and the inequalities (2) are not satisfied. Stable coexistence does not occur, but the model is neutrally stable. For example, in the two-species case, population densities approach the line $\alpha_{11}N_1 + \alpha_{22}N_2 = 1$, but can remain at any point on this line, until perturbed. In particular, there is no tendency for either species to increase from low density if perturbed there, and so there is no stable coexistence.

The significance of neutral models is their ability to predict some patterns of diversity seen in nature, for example in very diverse communities, neutral models have successfully reproduced the observed frequencies of species with different degrees of commonness and rarity [8]. To produce any pattern at all, however, they need to go beyond the strict deterministic description of equations like those in Table 1, and generally include demographic stochasticity. They thus recognize the finiteness of population size, and include independent chance events in the lives of individuals that determine individual fates [7]. For a model like the MacArthur consumer-resource equations, this would mean that the abundances of the species would be constantly randomly perturbed up and down the line $\alpha_{11}N_1 + \alpha_{22}N_2 = 1$, or with more than two species, over the hyperspace $\sum \alpha_{jj}N_j = 1$. Extinctions do occur in such models, and so in modern versions they include stochastic speciation and immigration to balance species losses [7].

The predictions of neutral models have often not held up [9-12], and neutral models do not give predictions about the differential effects that environmental change often has on the species in a guild [13], which are critical for conservation and management questions. On the other hand, models in which individuals of different species are not identical in their ecology can reproduce at least some of the patterns of multispecies diversity predicted by neutral models [34]. Neutral models provide a simpler mathematical route to some predictions, and in this way have highlighted some of the processes that lead to some observed patterns in nature, but these same processes are able to produce these patterns in nonneutral models as well.

2.3 Multitrophic diversity maintenance

Similar species can interact with one another by feedback loops through resources, or by feedback loops through predators. Naturally, they may also interact directly by interfering [35] with or facilitating each other's activities [36], or through intraguild predation [37]. However, the focus here is on the much misunderstood and critical area of feedback loops through predators [38]. Fig. 4 expands the foodweb model of Fig. 1 to include predators of the species in our guild of interest. Much emphasis has focused on idea that competition limits diversity of guild members, while predation modifies what competition does. For example, the keystone species idea was developed around the concept that predation on a competitive dominant would prevent competitive exclusion [39, 40].

The keystone species idea can be view directly within the competition framework above if it is assumed that the predator, in causing mortality, increases the resource maintenance requirement of the dominant species. This is a natural expectation because if a species has higher mortality, to persist it will need higher reproduction, and higher resource consumption to fuel that reproduction. The increased maintenance requirement for the dominant then decreases its κ value making it more comparable to that of other species, potentially enabling coexistence. For example, in the two-species case, the coexistence conditions (2) might become satisfied [6].

The above keystone species discussion focuses just on the mortality that the predators cause, and neglects the feedback loops associated with them. In causing mortality, the predator benefits and can build up in density, with the potential then of inflicting greater mortality. The feedback loops from guild members (the prey) to guild members arise because higher densities allow predator numbers to increase, increasing mortality on guild members. As Holt [38, 41] pointed out many years ago, these feedback loops through predators can have

very similar effects to feedback loops through resources. As consequence Holt coined the term “apparent competition” [41]. While previously we focused on species differences based on their use of resources, equally we can focus on species differences based on their patterns of susceptibility to the various predator species of the guild in question. Thus, the idea of a species’ niche can be expanded to include susceptibility to predator species [3, 5].

Within this expanded concept of a niche, the niche overlap measure ρ is extended to predator overlap too. Indeed, the MacArthur consumer-resource model extends to a consumer-resource-predator model, with ρ depending on both resource and predator overlap, measuring resource-sensitivity and predator-sensitivity similarities between species [16]. For example, ρ would be lowered if one species were more sensitive to changes in resource abundance while the other species were more sensitive to changes in predator-abundance. The extended fitness measure, κ , accounts for overall predation susceptibility as well as resource harvesting ability.

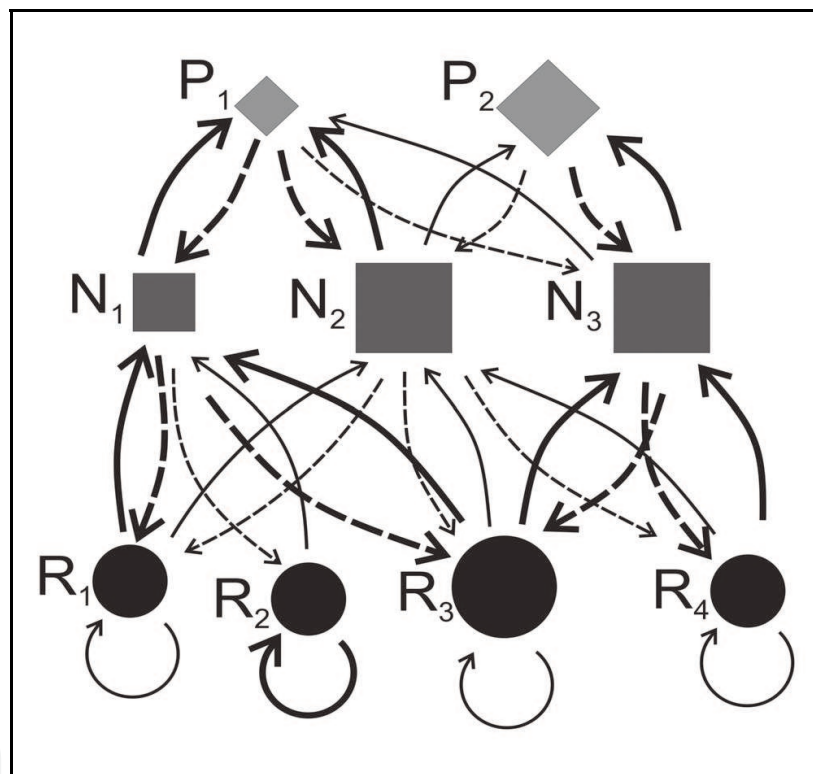


Fig. 4. Foodweb for the consumer-resource-predator model. As for Fig. 1, but with predators signified by the diamond symbols.

In this fuller concept of the niche, competition coefficients α_{ij} , and α_{jj} , become coefficients of interspecific and intraspecific density dependence, and thus include both resource competition and apparent competition. Of most importance, the relationship (1) between competition coefficient ratios, fitness ratios and niche overlap still holds, and the coexistence conditions (2) remain valid. Thus, no longer can competition and predation be regarded as having very different effects on species coexistence. We should not think of competition as the primary factor limiting coexistence, with predation modifying what competition does. Instead, the view emerging corresponds to Holt’s [38] advice that what is possible for competition is possible for predation too.

Relationships with resources and with predators can equally promote or limit diversity depending on the circumstances. Coexistence is promoted if different guild members have different relationships with their resources or different relationships with their predators, and exclusion is promoted if these relationships tend to be similar. Differences with respect to either resource sensitivity or predator susceptibility lower ρ , while similarities in either respect increase ρ . As noted above, an extra complication is that complementary relationships between species between sensitivity to resources and susceptibility to predators also lowers ρ , and is referred to in the literature as a competition-predation tradeoff [42].

Feedback loops through resources and through predators naturally do have some differences. For example, predators fitting the most common notion as species that hunt and kill prey species, are often larger than their prey, or of comparable size, and are normally less species rich than the prey they focus on, while the resources of their prey may be more species rich. Opportunities for niche distinctions between species due to their relationships with their predators would therefore seem less than the opportunities due their relationships with their resources. However, predatory behavior can be complex [43], and when predators have frequency-dependent behavior, a single predator has a similar effect in terms of the coexistence of prey species to several predators that do not have this frequency-dependent behavior, but are instead specialists on particular species. Moreover, interpreting “predators” as natural enemies more generally, such as diseases and parasites, makes predators appear every bit as able as resources to define distinct niches for their prey species.

The potential symmetry between resources and predators in promoting coexistence or exclusion depends also on the relative strengths of these processes. The niche overlap measure ρ takes these relative strengths into account. This can be seen in the formula in Table 1, where the reciprocal of the renewal rate of a resource weights its importance in the overlap measure. Slow renewal means that the measure is more strongly affected by consumption, and therefore more strongly contributes to resource competition. Similarly, in the extended overlap measure to include predation, the ability of a predator to build up in response to prey consumption weights its importance, and determines its contribution to apparent competition [16]. Of most significance, if resource separation is strong, but resource competition as a whole is weak relative to apparent competition, then that resource separation will have little effect on coexistence. Whether the species coexist depends on whether their niches are distinguished by predation. If their niches are not distinguished by predation, then they will have difficulty coexisting despite substantial separation at the level of resources. Naturally, the opposite conclusion is reached if it is resource competition that is strong relative to apparent competition.

2.4 Variation in time and space

All natural environments vary substantially in time or space in at least some major ecologically significant ways. Environmental variables and population densities nearly always vary substantially in both time and space. Empirical studies show this, but at great variance with the realities of nature, attention of theory to these facts historically was not a mainstream endeavor [44], and sadly that remains true today. Despite the absence of mainstream attention, considerable theory on the role of variation in time and space has been developed [14, 17, 19, 20, 38, 45-52]. Although the influence of this theory on empirical studies has not yet matched its potential importance, there is now a growing body of related empirical studies [53-56]

Some ideas about spatial and temporal variation, especially those under the heading of disturbance, have viewed variation in the same way that has often coloured thinking about predation: competition has been seen as limiting diversity, with variation in time and space as modifying or even nullifying what competition does [57-60]. Many of these views are influenced by the idea that variation in time and space make ecological communities “nonequilibrium,” while niche ideas are presumed to depend on the concept of equilibrium [61]. Nothing could be further from the truth [3, 5].

Theoretical studies converge on the conclusion that variation in time and space are best viewed as providing more opportunities for the niches of species to be distinguished, defined by the responses of species to the changing conditions they encounter [3, 5]. This is most easily understood with respect to spatial variation [50, 62-64]. If species favor different habitats, and their resources are consumed and regenerated locally in those habitats, the habitats provide separate feedback loops, just like separate resources. Separate feedback loops with respect to predators are less likely, because predators are often wider ranging than their prey and so prey densities in one habitat can affect predation in other habitats, but this case has been developed theoretically [38]. The same would be true of resources too if resources moved between habitats, or if habitats changed their status over time on a shorter time scale than resource changes, i.e. if there were rapid spatio-temporal environmental variation [65]. Similar issues apply to temporal variation [5].

Niche theory for spatial and temporal variation has developed techniques for assessing the extent to which spatial and temporal variation can separate the niches of species [20, 22]. This is the concept of covariance between environment and competition and its generalization to include apparent competition [51, 52]. Such covariances assess whether density-dependent feedback loops change with the environmental conditions under consideration, and can thus separate the niches of species. Based on them, powerful techniques for definitively testing diversity maintenance hypotheses based on spatial and temporal have been proposed [20] and implemented in some cases [22, 66]. Extension of these ideas for other niche-based diversity maintenance mechanisms should be possible, and might well lead to much progress on deciding between the various diversity maintenance ideas that have been proposed.

3. Conservation and management

Although it is not possible at the present time to say with confidence which of the many possible diversity maintenance ideas applies in any particular system, these ideas share enough features in common that some general advice is possible. Our principal example has been MacArthur’s consumer-resource model, and its extension to a consumer-resource-predator model, for which average fitness and overlap measures are easy to define. Per capita growth rates in these models are linear functions of the densities of the various species. Models similar in spirit, but having nonlinear relationships, have been studied extensively by Tilman [17, 67], especially for plants limited by nonbiological resources, and compared with others by Chase and Leibold [3]. Although these simple measures of average fitness and niche overlap are not available, the underlying concepts remain applicable [3]. Other models of resource and apparent competition in both constant and variable environments have yielded measures of fitness and niche overlap, when they have been sought explicitly [5, 29, 47, 51, 52, 68], clearly demonstrating how these ideas extend

beyond MacArthur's [27] beginnings. Moreover, Shigesada [69] provides an explicit representation of spatial competition models in the MacArthur framework.

The fact that different species do differ from one another ecologically means that changes in the environment do affect different species differently or to different degrees. Under the individual-species approach to conservation and management, this would simply mean that different species are at risk to different degrees from some change in the environment due to human activities. Under the interactive model given here, changes in the environment need not directly affect a species for it to be affected indirectly through its linkages with other species. The fitness measures κ reveal this most simply. A mortality rate of a particular species might be changed by hunting, elimination of a predator, or changes in physical stress in the environment. That change would have a direct effect on that species, either increasing or decreasing its abundance and perhaps putting it at risk, but that change would also have effects on a species' relationships with others. In particular, in the MacArthur model, we see that the ratio of the κ values would be affected. An increase in the κ ratio in one species favor disadvantages another, potentially leading to its extinction.

One example of this κ -ratio analysis is its application to understanding invasive species of large effect [30, 70]. A large κ value in a particular system would allow a species to invade that system, but would have also have the effect of depressing native species and potentially driving them extinct. There are a number of ways that an invasive species might achieve a larger κ value including low susceptibility to natural enemies in the invaded system [71], advantages in resource harvesting [72], and lower sensitivity to competition than the native species [73]. Alternatively, an invasive species might have a larger κ value than native species because habitat degradation has increased stresses on native species, lowering their κ values, and rendering the system vulnerable to invasion [30, 74]. Viewed from another perspective, a native species might become endangered not because some environmental change has directly affected it, but because other guild members have had their κ values elevated by changes that directly benefited them.

Naturally, changes in resource supply also have important effects [75]. Increasing the carrying capacity of a resource that one species depends on directly increases that species' κ value, and so can increase its ability to compete with another species that does not depend on that resource. This other species would thus be disadvantaged, potentially driving it extinct. However, not just average fitness, κ , but niche overlap, ρ , would be affected by the increase in supply of a particular resource because ρ depends on resource carrying capacities (see Table 1). In particular, ρ would decrease with an increase in the carrying capacity of a resource that only one species uses. Nevertheless, the change in the κ value has the larger effect confirming the conclusion that changes directly benefiting only one species will harm its competitors indirectly. Effects like this are most clearly seen for invasive species where an increase in resource supply, for example nitrogen deposition for an invasive plant species [76, 77], gives advantages to invaders, depressing native species. However, these concerns apply not only between invaders and native species but between native species where factors helping just some species may well negatively affect others in the same guild [75].

These various effects stemming from changes in resource richness have their counterparts in habitat availabilities because habitat variation in space can have effects similar to resource diversity, as explained above in the section on variation in time and space. Thus, increasing the availability of a habitat type specific to one species, can negatively affect another species that does not use that habitat type, but shares other habitat types with the species that does.

This outcome can be understood intuitively: one species increases in abundance when a valuable habitat type becomes more available, and, due to dispersal between habitat types, its abundance everywhere is increased. It thus has greater competitive effects on other species in all habitats. From the perspective of the theory above, average fitnesses and niche overlap change in the same way as when resource supply is changed. Similar effects apply to temporal environmental variation, an issue of particular concern with climate change [78]. For example, desert annual plants are believed to coexist with one another because different species are favored in different years, depending on the weather [19, 55]. Changes in weather patterns can change the relative κ values of the species if the weather becomes on average more favorable for some than for others. Changes in disturbance regimes can have similar effects through changes in the patterns of spatio-temporal variation [79].

Although systems where coexistence relies on disturbance are sometimes regarded as nonequilibrium [80], they do not escape these general principles. Individual species may be adapted to survive and even take advantage of temporal change, but there is every reason to expect that individual species, and the system as a whole, are sensitive to changes in the average frequency and intensity of environmental events, such as disturbances [81, 82]. Surviving and taking advantage of temporal change may rely on life-history attributes such as dormancy, but may also depend on dispersal to and from refuge habitats that escape change either permanently or at given time (e.g. when a fire sweeps through) [83]. Maintaining landscape connectivity, for example through maintenance of dispersal corridors, is especially important in such circumstances [84].

Finally, we come to the important question of trophic structure. Recognition that predation and competition can have similar roles in diversity maintenance, and that the effects that each has can be undermined by the other, depending on their relative strengths, means that maintenance of trophic structure is vital for conservation [85]. There is much concern about loss of large predators in many systems [86-89]. These predators are often valued for their own sake. Conservation measures focused on them might aim merely for their persistence in nature, rather than for maintenance of the roles that they have in systems [90, 91]. For example, practices in the United States relating to wolf restoration face contentious arguments over the mere persistence of wolves, versus maintaining their numbers so that the ecosystem roles are restored as well [92, 93]. Discussion of trophic cascades, which are increasingly seen in marine systems, as the larger species are eliminated, focus much on the overall abundance of a given trophic level [94, 95]. However, the theory discussed here emphasizes that decimating one trophic level will affect the diversity maintenance roles that it has in other trophic levels for which is either a predator trophic level or a resource trophic level, as has been found empirically in some systems [96].

4. Conclusions

Taken together, these principles and examples reemphasize that species should not be managed in isolation. Factors improving the situation for one set of species may degrade it for others. Maintaining trophic structure, physical environmental structure, disturbance regimes, and spatial connectivity are all common sense ideas that are backed up by the theory of diversity maintenance mechanisms.

5. Acknowledgements

This research was supported by NSF grant DEB-0542991.

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Research in Biodiversity - Models and Applications

Edited by Dr. Igor Pavlinov

ISBN 978-953-307-794-9

Hard cover, 364 pages

Publisher InTech

Published online 12, October, 2011

Published in print edition October, 2011

The book covers several topics of biodiversity researches and uses, containing 17 chapters grouped into 5 sections. It begins with an interesting chapter considering the ways in which the very biodiversity could be thought about. Noteworthy is the chapter expounding pretty original "creativity theory of ecosystem". There are several chapters concerning models describing relation between ecological niches and diversity maintenance, the factors underlying avian species imperilment, and diversity turnover rate of a local beetle group. Of special importance is the chapter outlining a theoretical model for morphological disparity in its most widened treatment. Several chapters consider regional aspects of biodiversity in Europe, Asia, Central and South America, among them an approach for monitoring conservation of the regional phytodiversity in India is of special importance. Of interest is also a chapter considering the history of the very idea of biodiversity emergence in ecological researches.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Peter Chesson (2011). Ecological Niches and Diversity Maintenance, Research in Biodiversity - Models and Applications, Dr. Igor Pavlinov (Ed.), ISBN: 978-953-307-794-9, InTech, Available from:

<http://www.intechopen.com/books/research-in-biodiversity-models-and-applications/ecological-niches-and-diversity-maintenance>

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